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Plant invasions in riparian areas of the Middle Danube Basin in Serbia

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Abstract

Riparian areas experience strong invasion pressures worldwide and represent important points of spread for invasive alien plants (IAPs) in the European mainland. The Danube Basin is a well-known point of high plant invasion levels. Given that the middle part of the Danube Basin is critically understudied and the general lack of data for Serbia, the study aimed to provide an insight into the spatial patterns of plant invasions in the riparian areas of Serbia (Middle Danube Basin area). A total of 250 field sites, distributed along 39 rivers (nine catchment areas) and six canal sections, were studied during a four-year period (2013–2016) for the presence and abundance of IAPs. At the landscape scale, we studied distribution patterns of IAPs, differences in invasion levels in different catchment areas and between rivers and canals. At the local scale, we investigated how the proximity to roads/railway lines, housing areas, different land-use types (primarily agriculture), and dominant vegetation on site related to invasion patterns. Of the 26 studied IAPs, those with a well-known weedy behavior, long history of cultivation and strong affinity for riparian areas prevailed in the study area. Riparian zones of the Danube catchment exhibited the highest invasion levels in terms of IAPs richness and abundance, followed by the catchment areas of the Timok, Sava and Zapadna Morava rivers. Surprisingly, the Danube-Tisa-Danube canal network had the lowest invasion level. At the local scale, agriculture in proximity of the field site and dominant vegetation on site were observed as significant predictors of the invasion level. On the other hand, proximity to roads/railway

lines and housing areas was not related to the invasion level. Finally, our study provides the first systematic overview of IAPs' distribution data for riparian areas of the Middle Danube Basin in Serbia, which could provide a basis for long-term monitoring of IAPs and development of future management plans.

Keywords
Alien plants, Danube, Danube-Tisa-Danube hydro-system, invasion corridor, invasive plants, riparian zone, river, waterway

Introduction

Estimates show that over 13,000 vascular plant species, approximately equaling the entire European native flora, have become naturalized outside of their native range (van Kleunen et al. 2015, 2019), with temperate and subtropical mainland regions of the world having the highest numbers of both naturalized and invasive (*sensu* Richardson et al. 2000) alien plant species (Essl et al. 2019). On a regional scale, habitat type is considered to be the best predictor of plant invasion levels (Chytrý et al. 2008a, 2008b; Chytrý et al. 2009; Pyšek et al. 2010), surpassing the importance of propagule pressure and climate (Chytrý et al. 2008a). Riparian areas are among the habitat types containing the highest numbers of invasive alien plants species (IAPs) (Vilà et al. 2007; Chytrý et al. 2008b).

Rivers and riparian areas are important hotspots of native species diversity (Ward et al. 2002), where a mosaic of different vegetation types (Hejda et al. 2015) provides a vast array of important ecosystem services (Pattison et al. 2017). However, these dynamic ecosystems (Naiman and Decamps 1997) are conflict zones (Vicente et al. 2011) exposed to numerous anthropogenic pressures and various disturbances (Tickner et al. 2001). The colonization of invasive alien species (IAS) has strongly affected European riparian areas over the past decades (Pattison et al. 2017). Given that riparian habitats are centers of IAPs diversity, they are consequently important potential sources of their outward spread (Tickner et al. 2001; Säumel and Kowarik 2010; Descombes et al. 2016; Arredondo et al. 2018), which usually starts along the watercourse and could expand further inland (see Burkart 2001).

For the European continent, Chytrý et al. (2009) have predicted that the lower Danube Basin area will be characterized by high levels of invasion and will show, in addition to the basin of the Po river, the highest presence of neophytes in Europe. Additionally, neighboring Hungary is an important invasion hotspot in Europe (Kröel-Dulay et al. 2019). However, there is a critical gap in knowledge about invasion patterns in the Middle Danube Basin – as holds true for the national scale in Serbia, both in studies on regional trends (Lambdon et al. 2008; Chytrý et al. 2009) and global databases on invasive species (EASIN, EPPO, NOBANIS, GRIIS, GLONAF). Meanwhile, various policies on global and European level have decreed goals and targets calling for action on IAS (Genovesi et al. 2014; Essl et al. 2020), including the zero draft of the post-2020 global biodiversity framework (CBD 2020), thus highlighting

the need for IAPs distribution mapping and monitoring (Latombe et al. 2017). Given this, our idea was to analyze how rivers of the Middle Danube Basin area have fared in respect to alien plant invasions.

Consequently, the study was designed to assess plant invasions in riparian zones of the Middle Danube Basin in Serbia. We analyzed (i) general invasion patterns, (ii) distribution patterns of dominant IAPs, (iii) differences in invasion levels between river and canal sites, and (iv) how site-specific factors (proximity of roads/railway lines, housing areas, land use in the vicinity of the field site and dominant vegetation on site) relate to invasion patterns. Additionally, analyzed IAPs were grouped, based on their origin and life form, to test how specific groups of IAPs relate to altitude. Finally, distribution data on the 26 IAPs is provided.

Methods

Study area

Serbia lies in the central part of the Balkan peninsula, covering a territory of 88,361 km^2. Its northern and southeastern parts are characterized by a continental climate, with cold winters and semi-arid summers, while its western parts experience a more humid, temperate climate. The eastern and central parts of Serbia are characterized by a semi-arid temperate-continental/sub-continental climate, with some transitional sub-Mediterranean elements (Stevanović and Šinžar-Sekulić 2009). While its northern low-lying part is a mosaic of hills, alluvial plains, river terraces and loess plateaus along the major rivers (i.e. Danube, Sava, and their left tributaries; Radulović et al. 2011), the southern part is mostly mountainous, except for major river valleys of the Velika Morava, Zapadna Morava, Ibar, Južna Morava, and Nišava rivers (Stevanović and Šinžar-Sekulić 2009).

The total length of all waterways in Serbia is 65,980 km, with a prevalence of small to medium rivers, not longer than 100 m. All rivers in Serbia belong to three main drainage basins. The Danube catchment area, belonging to the Black Sea drainage basin, covers 92.5% of the territory, containing also the longest rivers in Serbia: Danube, Sava, Tisa, Velika Morava, Timok, Mlava, and Pek, with many tributaries. The Adriatic Sea drainage basin occupies 5.4% of the territory, primarily consisting of the basin of the Beli Drim river, located mainly in the Metohija valley. The Aegean Sea drainage basin covers 2.2% of the total area of Serbia, with the Pčinja river being one of its three main rivers, located in the far southeastern part of the country (Gavrilović and Dukić 2014).

The Danube-Tisa-Danube (DTD) canal system is the greatest hydrotechnical complex made in Europe (outside of Russia), built in the period from 1728 to 1957 (Gavrilović and Dukić 2014). It was built in the northern, low-lying part of Serbia (the Vojvodina Province) as a multipurpose solution for flood control, irrigation, water supply for the industry, and various societal values, such as recreation, fishing, and

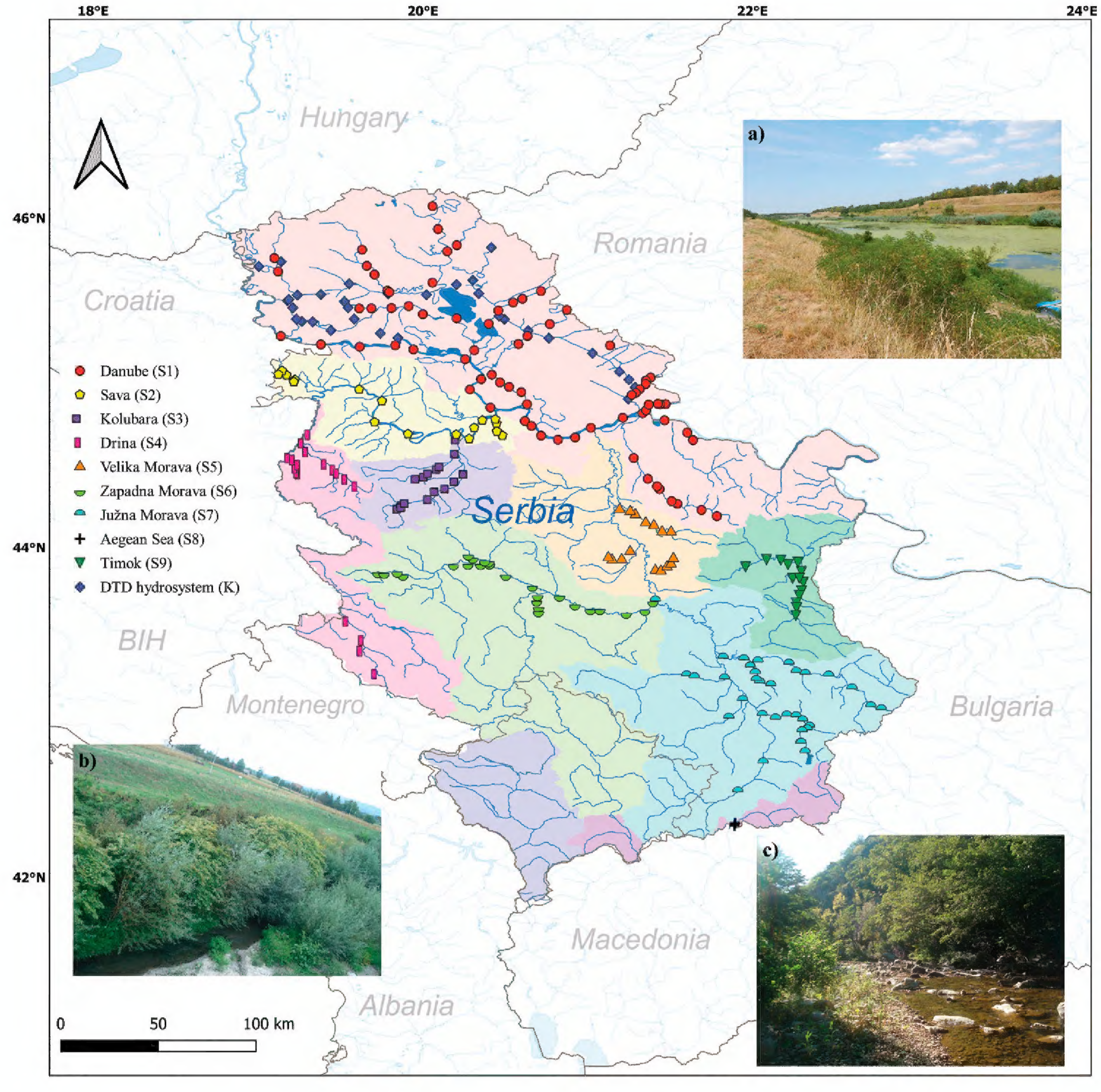

Figure 1. Distribution of field sites included in the analysis within different catchment areas of Serbia. Original photos of three selected field sites **a** - canal section of the Danube-Tisa-Danube hydro-system, loc. Vlajkovac **b** - river Čemernica, Zapadna Morava catchment area, loc. Konjevići **c** - Pčinja river, Aegean Sea drainage basin, loc. PIO "Dolina Pčinje".

navigation. The total length of all main and side canals in the network is 651.33 km, with 301.13 km located in the western Bačka region and 350.20 km in the eastern Banat region of the Vojvodina Province (Gavrilović and Dukić 2014).

Field research

Field research was carried out at a total of 250 field sites to cover all river catchments and the entire territory of Serbia (Fig. 1), i.e. all eight river catchments of the Black Sea drainage basin (Danube basin), the catchment area of the Pčinja river in the Aegean Sea drainage basin, and the Danube-Tisa-Danube (DTD) canal system (See supple-

mentary file 1), with a total of 39 rivers and six canal sections studied (217 and 33 field sites, respectively). Field sites along rivers and canals were uniformly distributed along the selected watercourses, with the distance between the field sites and their total number depending on the length of the studied watercourse.

Field research was conducted during the peak of the vegetation season (July-September) over four consecutive years (2013–2016). The timing of field research was selected based on the period when the studied plant species are fully developed and in full bloom. Based on preliminary findings from these field studies, 26 IAPs which occurred in at least three of the 250 surveyed field sites were selected for the analysis. We did not include *Portulaca oleracea* L. in this analysis, due to its uncertain geographic origins (but see Anđelković et al. in press for further details). The species selected for analysis are all listed in the preliminary list of invasive species in Serbia (Lazarević et al. 2012) and the Invasive species of Vojvodina database (IASV 2011).

Data collection

Vegetation data was collected on 100 m long longitudinal transects, set up parallel to the watercourse (following Aguiar et al. 2001, 2005), at approximately the same distance to the river. The transects were set up on the river/canal bank (Aguiar and Ferreira 2005) to better reflect the transitional nature of the riparian zone. Each longitudinal transect consisted of five 20 m long plots, aligned along the transect (modified by Aguiar et al. 2001). Cover of the recorded plant species was recorded (in percentage covers) in each plot, and the cover and abundance values were also assigned for each species according to the numerical van der Maarel scale (van der Maarel 1979) on the entire 100 m long vegetation transect. Plants were determined following the relevant literature, with their nomenclature following the Euro+Med PlantBase database (Euro+Med 2006–2020). Field data were georeferenced using the hand-held GPS Garmin eTrex 10 and distribution maps were made using QGIS software (QGIS Development Team 2009).

In order to test which site-specific conditions had a significant effect on the presence and abundance of the studied IAPs, a number of site-specific variables were tested against the total number and cover of IAPs per site. Data on the dominant vegetation type (broadleaf forest, tree plantation, shrub vegetation, herbaceous vegetation, bare land) and data on adjacent land use (housing areas, cropping land - field crops, pastures and meadows, primary natural habitat, industry) in the 500 m radius from the transect were recorded. These data were later verified, and amended if necessary, using original photographs from the field and Google Earth platform. Furthermore, distances to the nearest main road/railway track and housing area were measured, using the Google Earth platform.

Data analysis

The effects of dominant vegetation on the total number of analyzed IAPs and their total cover (of all target IAPs combined) were tested using one-way ANOVA, with dominant vegetation as a factor variable. To test for differences in invasion levels (expressed

as the total number of IAPs recorded on site) between the catchment areas one-way ANOVA was also applied, with catchment area as a factor variable. Results were then compared and separated using Tukey's honest significant difference test, with Levene's test used to ascertain the homogeneity of variance.

To test whether invasion levels were greater in river vs. canal sites, the total number of IAPs and their total cover on site were compared using the Student's *t*-test. The *t*-test was also used to compare invasion levels (expressed as the total number of IAPs recorded and their total cover) between field sites located in proximity (500 m radius) of a road/railway track, housing area and cropping land (field crops), and sites located at a distance over 500 m from these potential sources of propagules. Non-parametric Mann-Whitney U test was used to compare the total IAPs numbers in field sites located in urban zones vs. non-urban field sites.

Linear regression analysis was used to test for correlation between invasion level proxies (the total number of IAPs and their total cover) and altitude. Correlations between the total number of IAPs and their total cover and distances measured between the transect and the nearest road/railway track and housing area were also tested using linear regression analysis.

The database used for multivariate analysis consisted of 26 invasive alien taxa (Table 1). The dataset referring to the percentage covers of the analyzed taxa (averaged across the five plots within the transect), was used in two separate canonical correspondence analyses (CCA), related to altitude and distance from housing areas. Response curves fitted with a generalized additive model (GAM) were used to show how selected species are related to altitude and distance from housing areas.

For further analysis, two groupings of taxa based on percentage covers were done using the "trait averages" option. Taxa were first grouped based on their origin (Table 1), while the second grouping of taxa was done based on the IAPs life form (Table 1). These groups were analyzed in relation to altitude used as a nominal variable, using two separate redundancy analyses (RDA).

Univariate analyses were done using STATISTICA 7.0 and CANOCO (ver. 5.0, ter Braak and Šmilauer 2012) was used for multivariate analysis.

Results

General invasion patterns

A total of 1153 records of the selected IAPs have been documented in riparian areas of the analyzed rivers (Table 1). Of the analyzed IAPs, *Xanthium orientale* subsp. *italicum* was the most frequently documented and widely distributed, recorded on a total of 142 field sites (Fig. 2). The second most widely distributed was *Amorpha fruticosa* (Fig. 2), followed by *Erigeron canadensis* (Fig. 3), *Robinia pseudoacacia* (Fig. 2) and *Echinochloa crus-galli* (Fig. 2).

When the number of invaded rivers is analyzed per taxon, *R. pseudoacacia* and *X. orientale* subsp. *italicum* stand out, being recorded along the course of 92.3% and 89.7% of

Table 1. Number of records of the studied invasive plant taxa in different catchment areas in Serbia, with data pertaining to their life form and origin.

Taxon	code in the analyses	life form	origin	total number of records	number of records per catchment area									
					Danube (S1)	Sava (S2)	Kolubara (S3)	Drina (S4)	Velika Morava (S5)	Zapadna Morava (S6)	Južna Morava (S7)	Aegean Sea (S8)	Timok (S9)	DTD system (K)
Abutilon theophrasti Medik.	ABUTH	T	As	9	6	-	-	-	-	-	1	-	-	2
Acer negundo L.	ACRNE	P	NAm	27	19	3	-	-	2	1	1	-	1	-
Ailanthus altissima (Mill.) Swingle	AILAL	P	As	29	7	4	-	-	-	4	6	-	7	1
Amaranthus retroflexus L.	AMARE	T	NAm	75	34	5	1	4	6	11	8	-	1	5
Ambrosia artemisiifolia L.	AMBEL	T	NAm	85	29	10	12	6	2	8	4	-	1	13
Amorpha fruticosa L.	AMHFR	NP	NAm	108	47	10	1	3	5	6	11	1	10	14
Asclepias syriaca L.	ASCSY	G	NAm	6	2	1	-	-	-	-	-	-	-	3
Broussonetia papyrifera (L.) Vent.	BRNPA	P	As	6	2	1	-	-	1	-	-	-	-	2
Datura stramonium L.	DATST	T	C+SAm	14	8	-	2	-	1	1	1	-	-	1
Echinochloa crus-galli (L.) P. Beauv.	ECHCG	T	As	99	42	7	9	9	5	14	6	2	5	-
Echinocystis lobata (Michx.) Torr. & A. Gray	ECNLO	T	NAm	79	16	4	8	7	9	12	11	-	10	2
Eleusine indica (L.) Gaertn		T	mix	4	3	-	-	-	-	-	-	-	-	1
Erigeron annuus (L.) Pers.	ELEIN	T	NAm	57	25	2	4	2	1	4	4	-	2	13
Erigeron canadensis L.	ERICA	T	NAm	103	31	4	8	5	6	9	15	1	11	13
Fraxinus pennsylvanica Marshall	FRAPE	P	NAm	19	1	3	7	-	-	-	6	-	2	-
Helianthus tuberosus L.	HELTU	G	NAm	27	-	1	2	9	-	4	3	1	6	1
Parthenocissus quinquefolia (L.) Planch.	PARQU	L	NAm	12	5	1	-	-	2	-	-	-	2	2
Paspalum distichum L.	PASDI	T	trop	17	10	1	-	1	-	3	-	-	2	-
Phytolacca americana L.	PHYAM	G	NAm	13	3	-	1	-	-	4	3	-	2	-
Reynoutria×bohemica J. Chrtek & A. Chrtkova	REYBO	H	As**	12	-	3	1	4	-	4	-	-	-	-
Robinia pseudoacacia L.	ROBPS	P	NAm	102	18	5	10	8	7	17	19	2	9	7
Solidago gigantea Aiton	SOLGI	H	NAm	8	2	-	-	-	-	-	-	-	-	6
Sorghum halepense (L.) Pers.	SORHA	G	EuAs	47	19	4	2	2	2	8	1	-	-	9
Symphyotrichum spp.	SYMSP	H	NAm	45	10	2	6	3	6	1	10	-	2	5
Xanthium orientale L. subsp. *italicum* (Moretti) D. Löve	XANST	T	C+SAm	142	43	11	13	9	10	18	21	2	11	4
Xanthium spinosum L.	XANSP	T	SAm	8	2	-	-	-	-	-	-	-	-	6
Total number of IAPs in the catchment area				1153	384	82	87	72	65	129	131	9	84	110
Total number of field sites in the catchment area				250	74	17	17	18	16	25	34	2	14	33
Mean number of records per field site in the catchment area				4.61	5.19	4.82	5.12	4.00	4.06	5.16	3.85	4.50	6.00	3.33

* T – therophyte; P – phanerophyte; NP – nanophanerophyte; G – geophyte; H – hemicryptophyte; L – scandetophyte; As – Asia; NAm – North America; C+SAm – Central and South America; trop – Tropical; mix – Africa and Asia

** Hybrid species; origin assigned based on the origin of its parental species *R. japonica* Houtt. and *R. sachalinensis* (F. Schmidt) Nakai

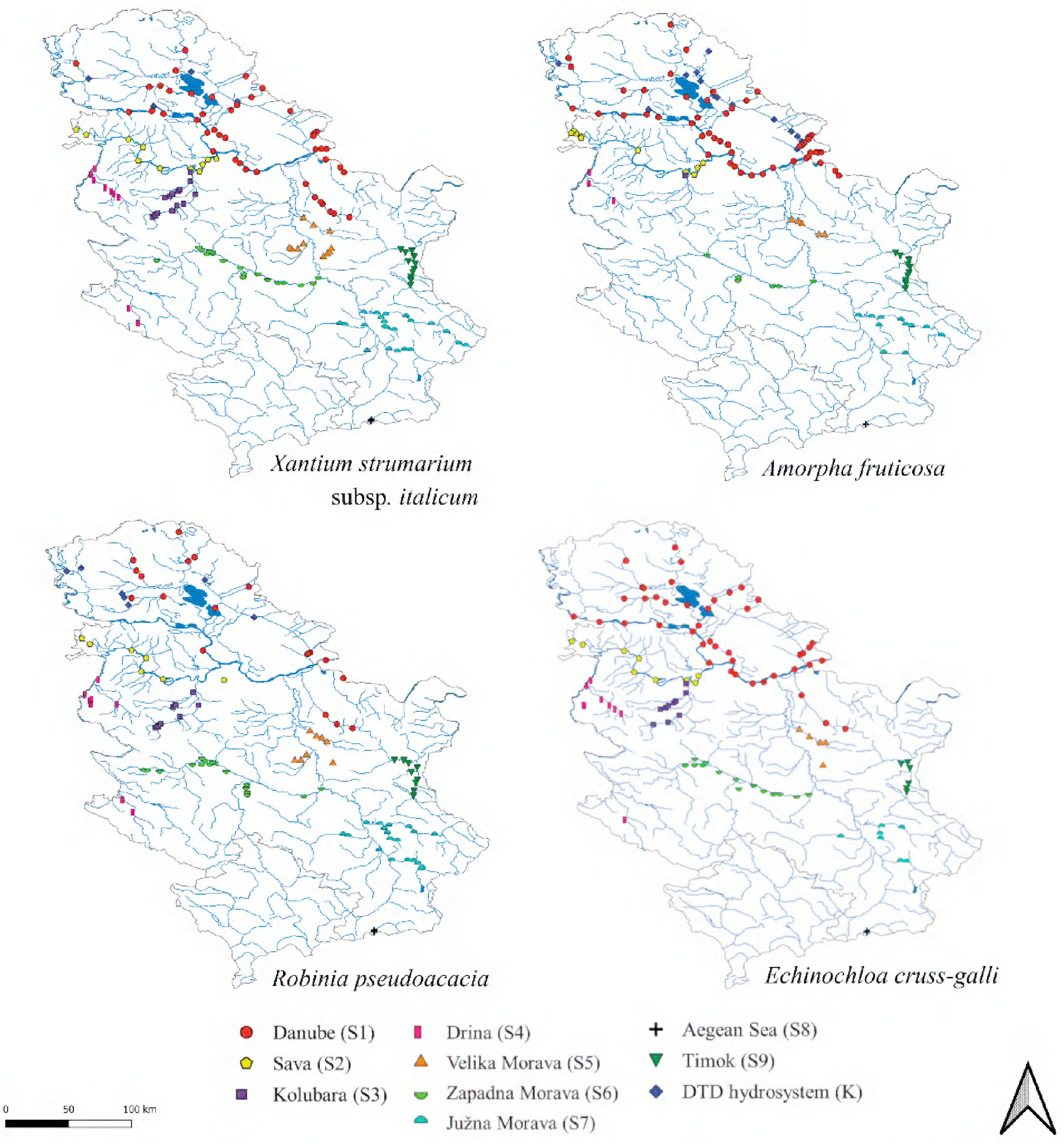

Figure 2. *Xanthium orientale* subsp. *italicum*, *Amorpha fruticosa*, *Robinia pseudoacacia* and *Echinochloa crus-galli* occurrences in the studied sites of riparian areas of Serbia. Invasive species distribution points relate to the survey areas shown in Fig. 1.

rivers, respectively. They are closely followed by *E. crus-galli* and *E. canadensis*, both recorded along 71.8%, and *A. fruticosa* in the riparian areas of 64.1% rivers (data not shown).

With regards to their origin, IAPs originating from North America were most frequent in the field, with 766 records (66.4% of total IAPs records; see Suppl. material 3). In terms of life form, therophytes were most frequent, with 692 records, followed by phanerophytes (183) and nanophanerophytes (represented by *A. fruticosa*; 108 records) (see Suppl. material 4).

The total number of IAPs per site was negatively correlated with altitude (r=-0.30, $p < 0.001$), as was their total cover (r=-0.19, $p < 0.01$). A generalized additive model revealed

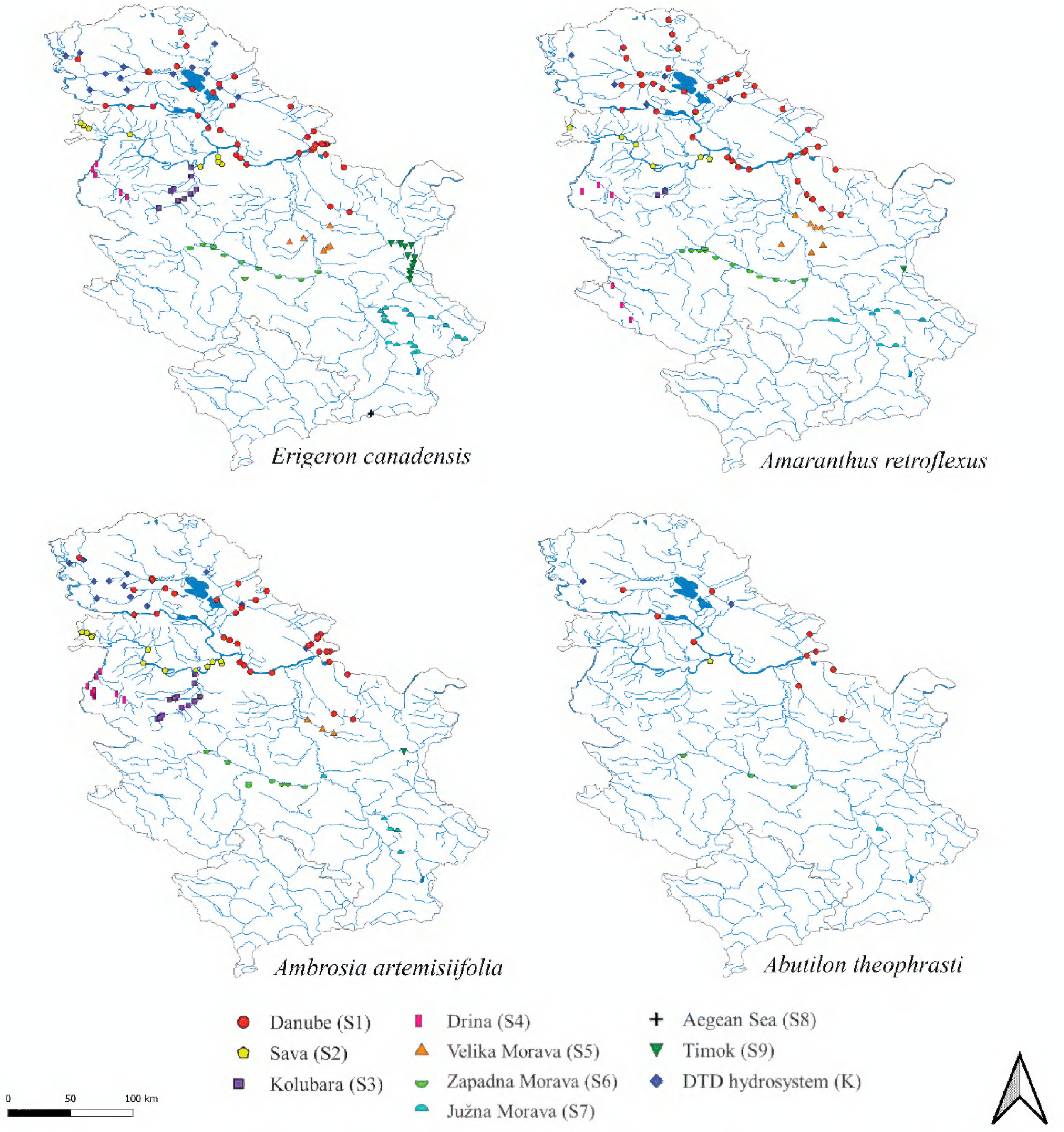

Figure 3. *Erigeron canadensis*, *Amaranthus retroflexus*, *Ambrosia artemisiifolia* and *Abutilon theophrasti* occurrences in the studied sites of riparian areas of Serbia. Invasive species distribution points relate to the survey areas shown in Fig. 1.

that altitude generally predicted individual IAPs cover on site (F = 7.1, p = 0.002). The abundance of *R. pseudoacacia*, *Helianthus tuberosus* and *Reynoutria* × *bohemica* was positively correlated with altitude, while the other IAPs' cover exhibited a negative correlation with this parameter (Fig. 4). A redundancy analysis (RDA; F = 2.4, p = 0.024) illustrated the relationship of IAPs grouped by origin and altitude. The results show that while all groups are more frequent at lower elevations (< 200 m a.s.l.), some (tropical, South American and mixed origin IAPs) were exclusively found here (for further details see Fig. 5). Redundancy analysis of IAPs grouped by life-form in relation to altitude (F = 5.0, p = 0.002) showed that while all groups dominated at lower elevations (<200 m a.s.l.), abun-

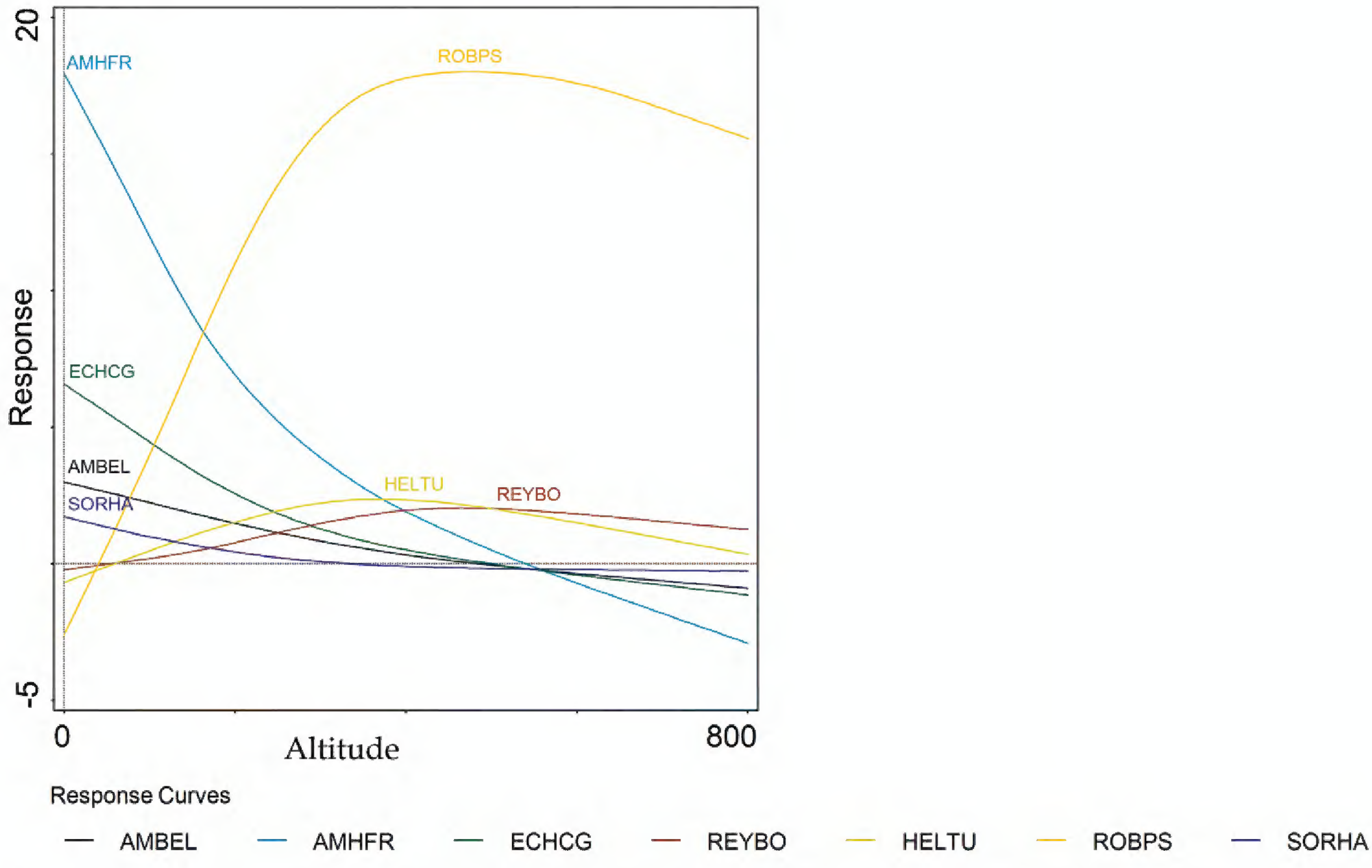

Figure 4. Response curves of the selected invasive alien plants in relation to altitude in the studied areas of Serbia. Names of taxa are abbreviated, see Table 1 for full names.

dance of geophytes (G), hemicryptophytes (H) and phanerophytes (P) became more pronounced in field sites between 200 and 500 m a.s.l. Phanerophytes (P) were the only group recorded more than others at altitudes between 500 and 800 m a.s.l. (Fig. 6).

Differences in invasion levels

Sites along rivers had significantly more IAPs than sites along canals (5.35±2.49 vs. 3.61±2.29, df = 248, p < 0.001; t-test). Similarly, the total cover (in %) of analyzed IAPs was significantly higher at river vs. canal sites (44.33±29.83 vs. 24.42±21.82, df = 248, t = 3.93, p < 0.001; t-test).

Catchment area had a highly significant effect on the total number of IAP records per field site (p < 0.001; See Suppl. material 5). The Timok catchment area (Eastern Serbia) had the highest mean number of IAP records per field site (6.14±0.64), followed by the Danube (5.88±0.28) and Sava (5.71±0.58) catchment areas. Meanwhile, the DTD canal system had the lowest mean number of IAP records per field site (3.39±0.42).

Effects of site-specific variables

Site-specific variables were differently related to invasion patterns in the study area. Sites in the proximity of roads or railways (< 500 m) had fewer IAP species, compared to the more distant sites (4.74±2.52 vs. 6.05±2.34, df = 248, t = 3.93, p < 0.001).

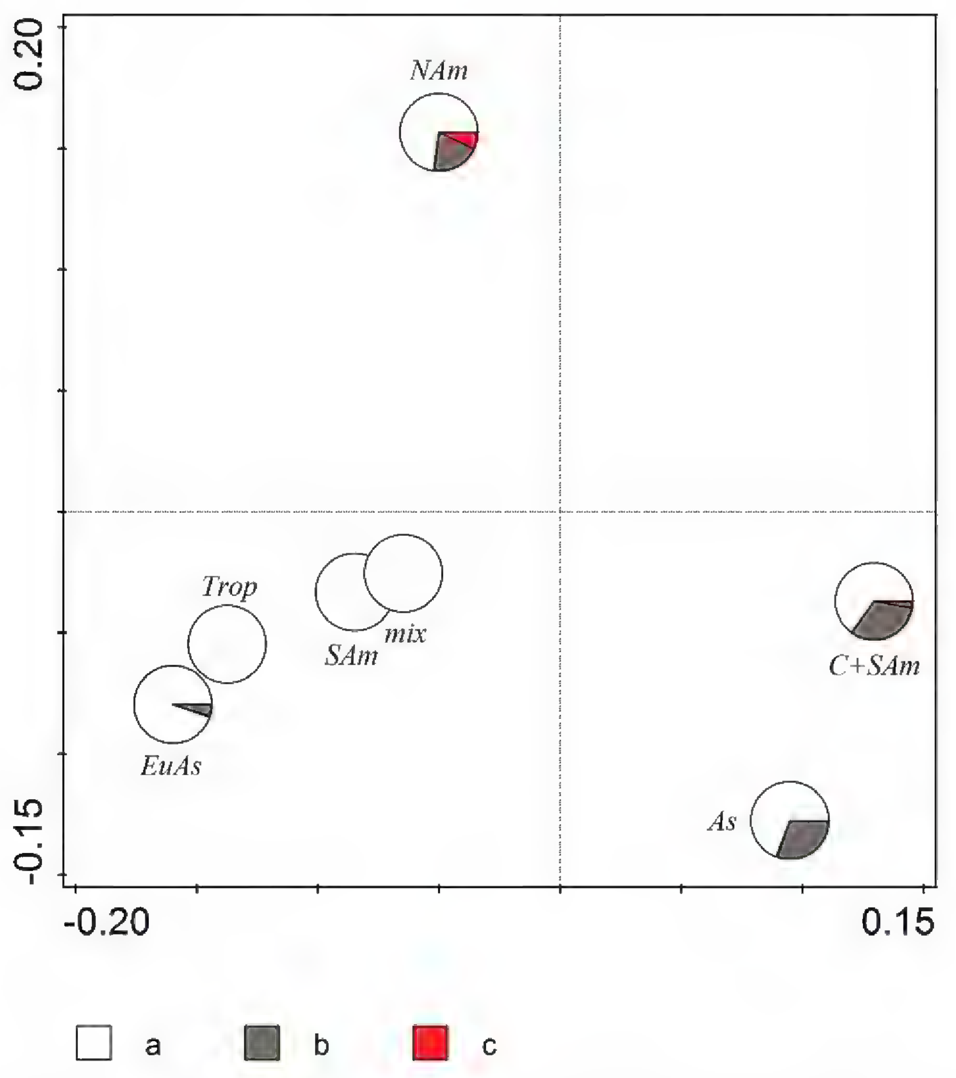

Figure 5. Pie chart diagram (RDA) showing the association of selected invasive alien plants grouped by origin with field sites categorized by altitude (a = < 200 m a.s.l.; b = 200 – 500 m a.s.l.; c = 500 – 800 m a.s.l.). Names of groups are abbreviated, please refer to Table 1 for full names.

Thus, an increase in distance from the road/railway track was positively correlated with IAPs number ($r = 0.18$, $p < 0.001$).

The proximity of housing areas did not have a significant effect on the total number or total cover of IAPs per site (See Suppl. material 6). Furthermore, distance from housing areas and the IAPs number were not significantly related ($p > 0.05$). However, the CCA showing distance from housing areas in relation to the cover of individual IAPs was significant ($F = 2.0$, $p < 0.01$) and response curves of the selected species are shown in Fig. 7.

Sites located in proximity of agricultural land (< 500 m) had more IAP species, compared to the more distant sites (5.26 ± 2.6 vs. 4.51 ± 2.25, df = 248, t = 2.03, $p < 0.05$). On the other hand, contrary to our expectations, there was no significant difference ($p > 0.05$; Mann-Whitney U test) in the number and cover of IAPs per site between field sites located within an urban zone and those found outside of cities.

The total cover of studied IAPs per site was significantly different ($p < 0.01$) between sites with different vegetation types (See Suppl. material 5). The lowest cover of IAPs, on average, was found for field sites dominated by bare land (14%) and a mix of broadleaf forest and shrub vegetation (28.8%), while field sites with dominant shrub vegetation had the highest cover of IAPs (49.4%). The dominant vegetation type was not significantly related to the total IAP species number ($p > 0.05$).

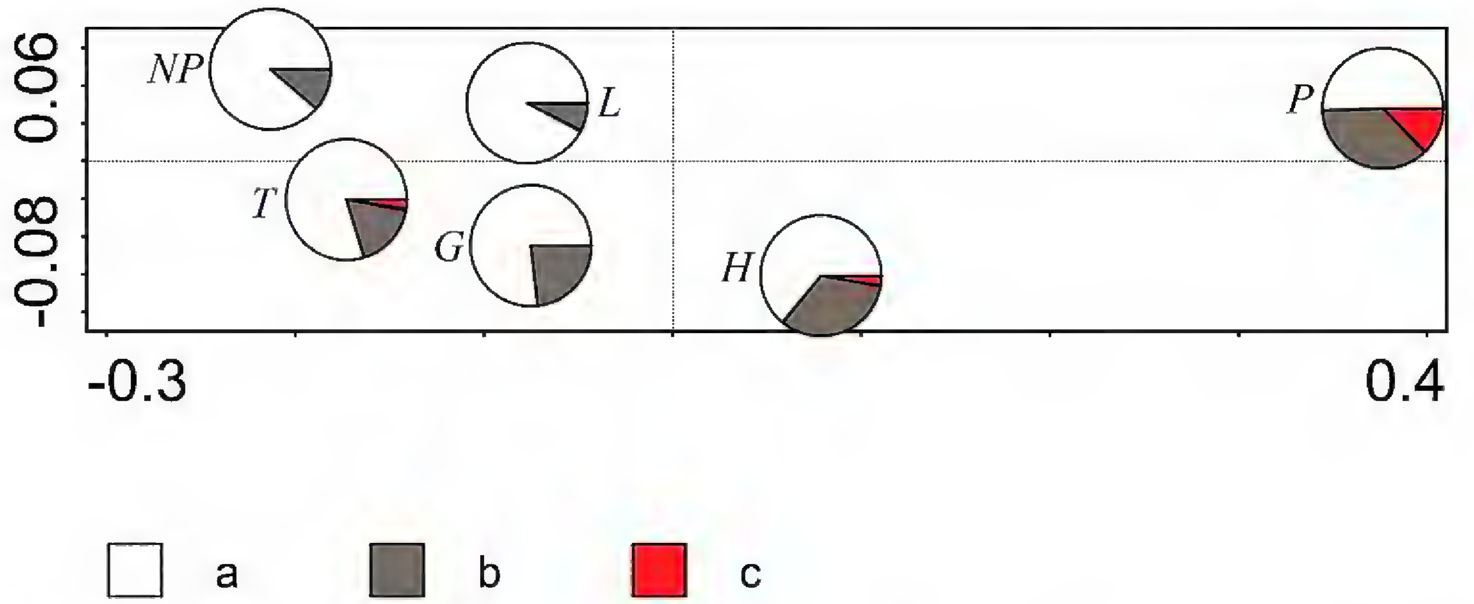

Figure 6. Pie chart diagram (RDA) showing the association of selected invasive alien plants grouped by life form with field sites categorized by altitude (a = < 200 m a.s.l.; b = 200 – 500 m a.s.l.; c = 500 – 800 m a.s.l.). Names of groups are abbreviated, please refer to Table 1 for full names.

Discussion

This study provides the first systematic overview of plant invasion patterns and IAPs distribution data for riparian areas of the Middle Danube Basin in Serbia. General invasion patterns, differences among catchment areas, and among individual invasive species were detected. Additionally, we also show which site-specific variables were related to invasion patterns.

General invasion patterns

Results pertaining to the relevance of species' origin and life form are consistent with those reported for other riparian systems (Schnitzler et al. 2007; Nucci et al. 2012; Liendo et al. 2015; Lapin et al. 2019). Species originating from North America, followed by Asian species, were the most frequent (See Suppl. material 3), as were annual species (therophytes; See Suppl. material 4).

The overall decrease in alien species richness with increasing altitudes is a well-known phenomenon, recorded worldwide (Pyšek et al. 2005; Chytrý et al. 2009; Liendo et al. 2015; Vorstenbosch et al. 2020). Moreover, the tendency of the majority of studied IAPs to favor lowland riparian sites (Fig. 4, 5 and 6) falls in line with previous studies (Schnitzler et al. 2007; Pattison et al. 2017; Lapin et al. 2019; Giberti et al. 2021). It has been argued that the effect elevation has on IAPs distribution and abundance is linked to the climatic conditions of their native ranges (Chytrý et al. 2005; Schnitzler et al. 2007) and temperature range of the invaded area (Skálová et al. 2015). Furthermore, unlike lowland areas, the mountainous areas are subject to fewer anthropogenic activities and consequently fewer disturbance events and lower propagule pressure, making them less prone to invasion (Nucci et al. 2012; Liendo et al. 2015). These effects are reflected in the abundance of the studied IAPs groups (Fig. 5 and 6). An exception to this general tendency are *R.* × *bohemica* and *H. tuberosus* (Fig.

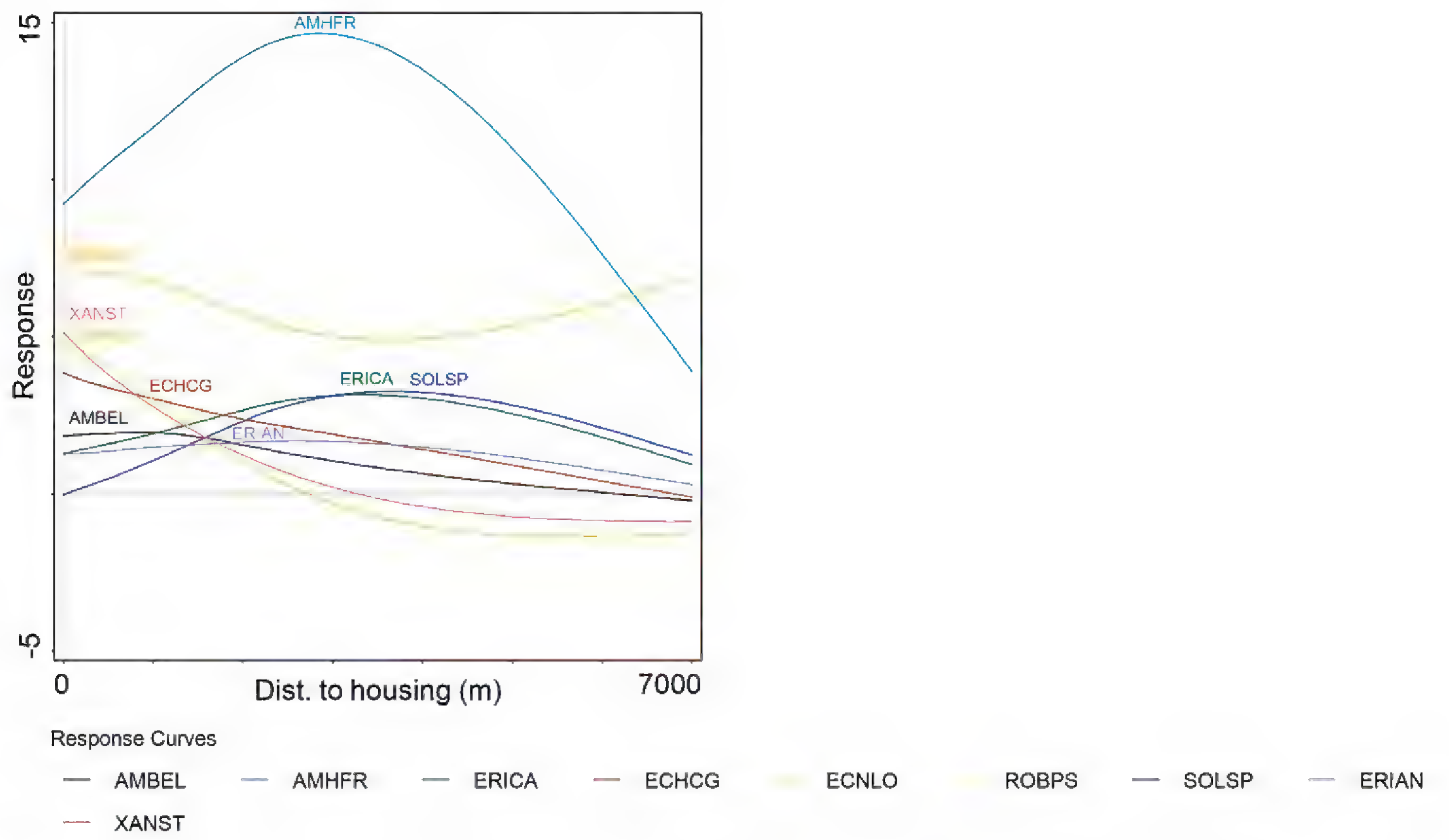

Figure 7. Response curves of the selected individual invasive alien plants in relation to the distance to housing areas. Names of taxa are abbreviated, see Table 1 for full names.

4, but also reflected in Fig. 6), and their association with altitudes between 200 and 500 m a.s.l. This association echoes their invasion along rivers in the Drina and Zapadna Morava catchment areas (field obs.). The presence of *R. pseudoacacia* at altitudes between 500 and 800 m a.s.l. reflects its cultivation history since it had been planted there for decades to stabilize the riverbanks (Nicolescu et al. 2020).

Differences in invasion levels across catchment areas

This study has found significant differences in invasion levels between the studied catchment areas, highlighting the catchment areas of the Timok and Danube rivers as the most invaded overall. Such findings are consistent with other studies denoting the Danube as an important plant invasion corridor (Stevanović et al. 2004; Paunović et al. 2015; Anđelković et al. 2016; Wagner et al. 2020). The highly invaded Timok river catchment area, geographically a part of the Carpathian massive, seems to be experiencing a similar increase in invasion levels already observed in the Carpathian Mountains of Ukraine (Simpson and Prots 2013). On the other hand, some field sites were uninvaded thus far, including several in the Južna Morava catchment area (Table 1). In this sense, three invasion-free field sites along the Vlasina river are an important finding, as a large portion of this river is protected under a range of national and international legislature, due to its conservation value (Amidžić et al. 2018).

Surprisingly, results have shown that the canal network of the Danube-Tisa-Danube hydro-system is the least invaded of the analyzed catchment areas. Such invasion levels along the canals are contrary to general expectations, given that field sites along the canal network

are under strong and constant anthropogenic pressure. Additionally, they are found within an entirely agricultural landscape of the Vojvodina Province and consequently experience seasonal nutrient-enrichment, due to N leaching from the surrounding agricultural fields (Hejda and Pyšek 2006). Finally, these results are especially surprising considering the effect agriculture had on invasion levels in the study area (See Suppl. material 6).

The observed invasion tendencies on river vs. canal sites could potentially be explained by the management regime which is being undertaken by the stakeholders in charge of the DTD canal network upkeep. While the banks of the DTD canal system are under a regular management system (mowing), riverbanks are mostly free from this form of anthropogenic control and IAPs are therefore allowed to spread unchecked. Such a situation could suggest that traditional management regimes still being employed along the canal banks control the spread of IAPs along canals. Regardless, all management plans need to take into account those species where management activities such as mowing (*R. × bohemica*; Jones et al. 2020) and coppicing (*R. pseudoacacia* and *A. altissima*; Brundu et al. 2020) are counterproductive, actually encouraging the further spread of IAPs.

Invasion patterns of the dominant IAPs

Our results on the most frequent and most abundant IAPs (Table 1; Figs 2 and 3) concur with other riparian and wetland area studies from Serbia and SE Europe (Török et al. 2003; Oprea and Sîrbu 2006; Čavlović et al. 2011; Krstivojević et al. 2012; Batanjski et al. 2015; Radovanović et al. 2017; Stanković 2017; Tmušić et al. 2019).

Amorpha fruticosa was recorded as the second most frequent IAP (Table 1, Fig. 2), which echoes its presence in other European riparian systems (Zavagno and d'Auria 2001; Dumitraşcu et al. 2013). Similarly, *R. pseudoacacia* was recorded at over 90% of the studied rivers (Fig. 2). The distribution of this species reflects its long-term cultivation history in Europe, and consequently Serbia (see Fig. 1 in Vítková et al. 2017). In fact, this invasive species is still being planted in Serbia, as a forest crop in the Danube River floodplains (Andrašev et al. 2015). Such practices have resulted in an area of over 150,000 ha under *R. pseudoacacia* in Serbia (c.f. Nicolescu et al. 2020), supporting further invasions by this species.

Finally, some of the most frequent IAPs in riparian areas (*X. orientale* subsp. *italicum*, *E. canadensis*, *E. crus-galli*, *Amaranthus retroflexus*, *A. artemisiifolia*) are also widely distributed in ruderal and agricultural areas of the region and spread intensively across the Balkans and SE Europe (Török et al. 2003; Weber and Gut 2005; Šilc et al. 2012; Kröel-Dulay et al. 2019). This could support the invasion of riparian habitats by these species.

The rather constrained distribution of *Asclepias syriaca* in the riparian areas of Serbia was an unexpected result, given that previous research (Vrbničanin et al. 2008b; Popov 2016; Stanković 2017) has revealed it to be widespread, especially in the northern parts of Serbia, with a strong tendency for expansion along watercourses (Popov 2016). Results were similarly surprising regarding the frequency and distribution of *R. × bohemica*, bearing in mind its strong preference for riparian habitats (Bailey and Wisskirchen 2004; Mandák et al. 2004; Bailey et al. 2007) and its current distribution in Serbia (Jovanović et al. 2018). Despite the low number of records observed in this

study, it needs to be pointed out that Jovanović et al. (2018) have shown that in SE Europe, Serbia has the highest number of appropriate habitats (primarily riparian) for further expansion of *R.* × *bohemica*.

Effects of site-specific conditions

Local site conditions determine the susceptibility of a field site to invasion (Chytrý et al. 2008b). In this sense, certain land use types, particularly agriculture, proximity of transport infrastructure (i.e. roads and railway lines) and degree of urbanization are expected to favor the presence and dominance of IAPs (Chytrý et al. 2008b; González-Moreno et al. 2014; Benedetti and Morelli 2017; Horvitz et al. 2017; Rat et al. 2017).

Agriculture, as land use type observed in the 500 m radius from the studied field site, was an important predictor of IAPs richness (See Suppl. material 6). Such observations echo the effects propagule pressure (originating from agriculture, both field crops and backyard gardens/orchards) and constant influx of vast amounts of nutrients have on the presence and abundance of IAPs. These results align with studies highlighting the role of agriculture in the spread of alien plant species (Osawa et al. 2013; González-Moreno et al. 2014, 2017) and the fact that the majority of alien plant taxa was introduced to this area as contaminants in seed material and nursery saplings (Anačkov et al. 2013). Furthermore, some of the most frequently recorded IAPs in the field are among the most frequent agricultural weeds in SE Europe (Šilc et al. 2012; Follak et al. 2014; Kröel-Dulay et al. 2019), highlighting the importance of agriculture as a source of plant invasions in the Middle Danube Basin area.

Surprisingly, we did not detect a link between the proximity of roads/railway lines and the number of observed IAPs per site. The role of these transport corridors in the spread of invasive plants is generally well-known (Rouifed et al. 2014; Bacaro et al. 2015; Benedetti and Morelli 2017). As roadside spread of alien plants at higher elevations has recently been observed (Vorstenbosch et al. 2020), a similar trend could occur in those riparian areas (> 500 m a.s.l.) in Serbia which are positioned close to main roads.

No effects were observed between the proximity of field sites to housing areas, or their position in urban areas, and the level of invasion. This was unexpected, given the importance of urbanization for plant invasions (Horvitz et al. 2017). Furthermore, Jehlík et al. (2019) and Rat et al. (2017) have also shown that urban areas along rivers harbor high numbers of neophytes.

This study showed that dominant vegetation on site is a significant predictor of the total cover of studied IAPs. Riparian field sites dominated by shrub vegetation had the highest recorded cover of invasive plants, which aligns with other studies showing that riverine scrubs are characterized by the highest proportions of IAPs (Vilà et al. 2007; Chytrý et al. 2008a, b; Stanković et al. 2019). The presence of IAPs on field sites dominated by bare land could have implications for the future and needs close monitoring, as such bare grounds (e.g. river bars or recently disturbed grounds) represent perfect venues for the incursion of invasive plants in riparian systems (see Liendo et al. 2021 and references therein).

Consequently, we can surmize that agriculture and dominant vegetation on site override the importance of proximity of transport infrastructure and housing areas (as human-related factors *sensu* Horvitz et al. 2017) at the local scale. It can also be theorized that, in addition to agriculture, the river-mediated dispersal of propagules (Pyšek and Prach 1993; Richardson et al. 2007) could also be considered as an important source of invasive plants in the study area, which should be tested in future studies.

Conclusion

Our study revealed differences in invasion levels between catchment areas of the Middle Danube Basin area. The Timok and Danube catchment areas were shown to support highest invasion levels. While some catchment areas (e.g. Sava and Zapadna Morava) also had high numbers of IAPs, other were less subjected to invasions. The results presented here have important practical implications and can support the development of future management plans for the control of IAPs in riparian areas of both rivers and canals in the region. Furthermore, we believe that our results, in addition to their local and regional value, will contribute to documenting the invasion trends of IAPs in riparian areas of the Danube Basin and this part of Europe. Finally, this snapshot study, with well-defined survey areas, could serve as a basis for long-term monitoring of IAPs, which is critically needed for supporting the prioritization of management and conservation actions (Pergl et al. 2020).

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Supplementary material 1

List of the studied rivers/canal sections and their catchment area affiliation (and code in the analysis)

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Data type: List of rivers included in the filed word.

Explanation note: This file presents a comprehensive list of all the rivers which were included in the analysis. It is included as supplementary data as it provides additional information on the watercourses which were included in the analyses.

Link: https://doi.org/10.3897/neobiota.71.69716.suppl1

Supplementary material 2

Geographical distribution data of the studied invasive alien speces

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Data type: (measurement/occurrence/multimedia/etc.)

Explanation note: This file includes 26 tables containing geographical distribution data of the analyzed invasive alien plat taxa. In addition to latitude and londiude, data is also provided on the locality, watercourse along which data was recorded and the catchment area this watercourse belongs to.

Link: https://doi.org/10.3897/neobiota.71.69716.suppl2

Supplementary material 3

Figure S3

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Data type: Tiff file.

Explanation note: Origins of the analyzed invasive alien plants in the riparian areas of Serbia (expressed as the percent of records per each group).

Link: https://doi.org/10.3897/neobiota.71.69716.suppl3

Supplementary material 4

Figure S4

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Data type: Tiff file.

Explanation note: Biological spectrum of the analyzed invasive alien plants in the riparian areas of Serbia (expressed as the percent of records per each group).

Link: https://doi.org/10.3897/neobiota.71.69716.suppl4

Supplementary material 5

Tables

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Data type: Docx file.

Explanation note: Results of one-way ANOVA analyses, and subsequent Tukey's HSD post hoc tests.

Link: https://doi.org/10.3897/neobiota.71.69716.suppl5

Supplementary material 6

Table

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Data type: Docx file.

Explanation note: Mean total numbers of invasive alien plants recorded per site and their total cover values (± SD) in field sites depending on their proximity to main road/railway track, housing and adjacent land use types (cropping land, field crops, pastures and meadows, primary natural habitat, industry).

Link: https://doi.org/10.3897/neobiota.71.69716.suppl6